RESPIRATORY RHYTHM IN THE ELASMOBRANCH, *SCYLLIUM CANICULA*

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The ease with which respiratory reflexes may be elicited by stimulation of the surface of the pharynx and gills in fishes led early investigators to look for a reflex control of respiration in these vertebrates. Schoenlein (1895) perfused the gills of *Torpedo* and *Scyllium* through the spiracle and found the respiratory rate to increase with increased flow of water until, with too great a flow, the regular rhythm ceased and ejection reflexes occurred. If the flow of water was stopped, there were a few respiratory movements until all the water in the gills was pressed out, when complete passive inhibition of respiration occurred. Since this author observed no signs of dyspnea during perfusion with oxygen-free sea water for twenty minutes, he came to the conclusion that the control of respiration was mainly reflex. Bethe (1903) perfused the gills of *Scyllium canicula* and *S. catulus* both with oxygen-free sea water and with sea water saturated with carbon dioxide, and found that the rate and strength of respiration remained unaltered for about forty minutes, after which it began to be slower and weaker. He also paralyzed the peripheral receptors of the gills and pharynx with cocaine and obtained a cessation of respiration. He therefore concluded that the gas content of the blood, which in the higher vertebrates plays such an important part, is without influence in fishes, and that breathing is caused by peripheral stimulation.

Since these conclusions contradicted the results of Duncan and Hoppe-Seyler (1893), who determined the level to which the oxygen content of the water could fall before signs of disturbed respiration occurred in fishes, Baglioni (1907–08) investigated the reflex respiratory mechanism in both teleosts and elasmobranchs. He found that the respiratory inhibition which occurred on stopping the flow of water was not absolute, and he believed it to be a reflex due to air in the pharynx. He also found that fishes which were allowed to swim freely in evacuated sea water showed a marked increase in respiratory rate, extreme dyspnea, and periodicity. He concluded that it is a general property of the central nervous system in all vertebrates to react to oxygen lack by increased irritability.

The present paper is concerned with the respiratory responses which occur when the flow of blood through the respiratory center is stopped, and also with the effect of altering or stopping the flow of water through the gills.

Method

Vigorous specimens of the dogfish, *Scyllium canicula*, averaging 300 grams, taken during the months of March and April from the Bay of Naples, were used. The fish was taken out of water and the fore-brain was separated from the rest of the brain by a transverse cut just in front of the optic lobes and destroyed. The spinal cord was transected at various levels between the third and twelfth vertebræ and pithed posteriorly in order to keep the fish quiet. The animal was then placed ventral side up on a fish holder and the gills were perfused through the mouth. Respiratory movements soon became regular. The heart was exposed through the ventral wall of the pericardial chamber and a small gold hook was put through the superficial tissue at the tip of the ventricle. By means of a thread and a light writing lever its movements were recorded. A similar hook passed through the anterior border of the third or fourth gill slit was attached to a thread, passed horizontally to a pulley, and up to a light writing lever for recording respiration.

The perfusion water was taken from three large glass bottles placed 60 cm. above the fish holder. The rate of flow was controlled by means of a glass cock on each outflow tube near the bottle, and another near the mouth of the fish.

In certain experiments the aorta was transected at its junction with the conus arteriosus.

Results

A sudden alteration in the rate of flow of water to the gills evoked a reflex respiratory response and generally cardiac inhibition. The immediate effect of suddenly stopping and starting the flow or of increasing and decreasing the rate was respiratory inhibition, usually followed by one or more rapid and vigorous contractions of the gill muscles during which water was ejected from the mouth as well as from the gill slits. This ejection reflex occurred both when additional water was suddenly turned on and when the water was suddenly stopped (Fig. 1, *A* and *B*). A similar response to abrupt alteration in water supply to the gills occurred after the aorta had been transected to prevent any possible blood pressure effects through changes in water pressure on the gill vessels.

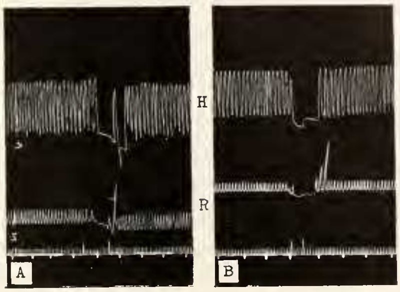

FIG. 1. Reflex cardiac and respiratory responses. In this and in subsequent figures the upper tracing is a record of the heart beat. The middle tracing records respiration. The large divisions on the time-signal record are ten seconds. *A*, perfusion of the gills suddenly stopped and started. *B*, flow of perfusion water quickly increased and decreased.

When the rate of flow was changed gently from 200 cc. per minute to 400 cc., there was an increase in both respiration rate and heart rate. If the flow was then reduced to the original, there was a return to the previous heart and respiratory rates (Fig. 2). In this case the heart rate before the change was 25 per minute, and the respiratory rate was 21. During a flow of 400 cc. per minute they were 42 and 27, respectively. A return to 200 cc. per minute gave 22 and 21, and a second increase to 400 cc. resulted in a heart rate of 42 and a respiratory rate of 31. Too great an increase, however, produced an irregularly inhibited rhythm of both the heart and the respiration.

When the flow of water was stopped for a period of several minutes, there was usually a temporary inhibition of both respiration and heart, followed by a slower rhythm which was sometimes very regular (Fig. 3) and sometimes showed a tendency toward periodicity (Fig. 4). With further continued lack of water the regularity of respiration was interrupted from time to time by generalized reflex muscular responses from the remaining parts of the central nervous system, during which both respiration and heart were irregularly inhibited. The medullary centers remained reflexly functional for over three and one-half hours.

The immediate result of transection of the aorta at the conus arteriosus was inhibition of both respiration and heart. But in a minute or two both began rhythmical activity although somewhat slower. Even without perfusion of the gills, regular respiratory movements occurred for a variable length of time. Figure 5*A* shows the

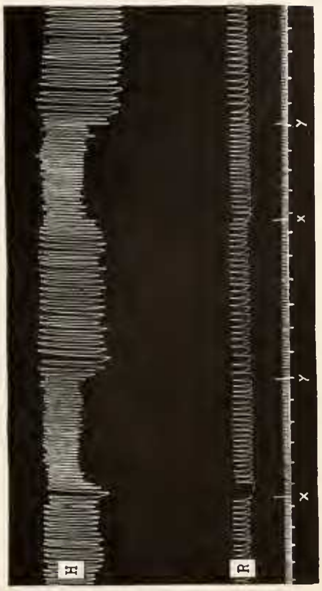

FIG. 2. Cardiac and respiratory responses to changes in the rate of flow of perfusion water to the gills. *X*, from 200 cc. per minute to 400 cc. *Y*, from 400 cc. to 200 cc.

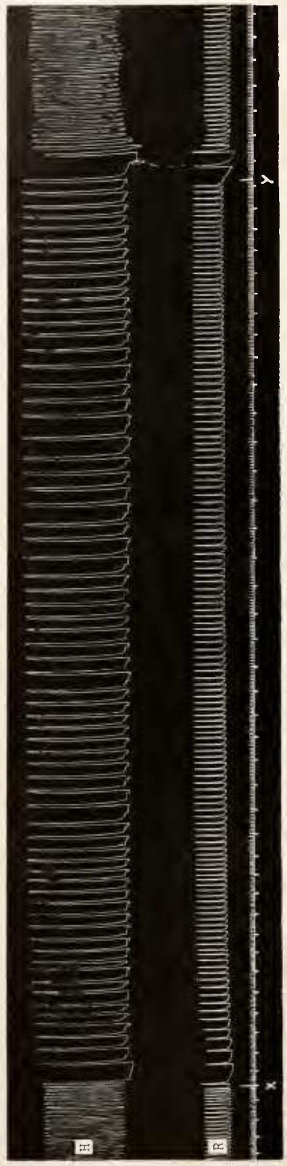

FIG. 3. Perfusion water to the gills stopped from *X* until *Y*, a period of 6 minutes and 32 seconds. Regular respiratory rhythm.

regular respiratory rhythm becoming periodic about ten minutes after transection of the aorta. Figure 5*B* was taken from the same fish

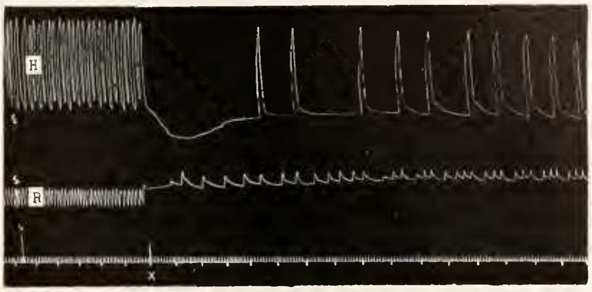

Fig. 4. Perfusion water to the gills stopped at *X*. Onset of periodic respiration after 90 seconds.

fifty-three minutes after the aorta was cut. A periodic series of dyspneic respiratory movements occurred followed by a weaker and

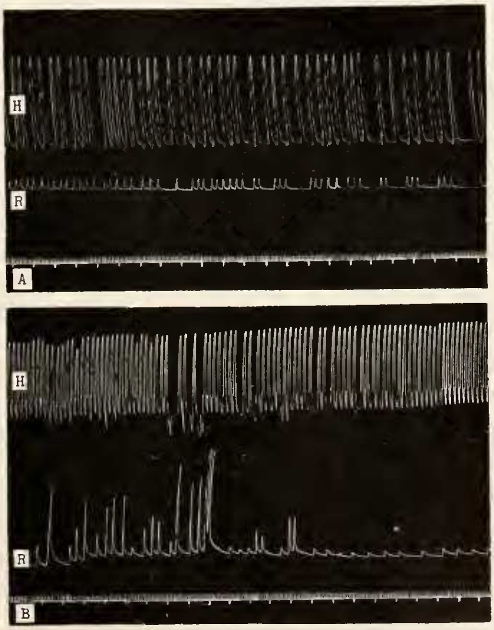

Fig. 5. Aorta transected at the conus arteriosus and perfusion of the gills stopped at the same time in a fish with the cord destroyed posteriorly from the fourth vertebra. *A*, record of heart and respiration beginning ten minutes after transection of the aorta, showing the onset of periodic respiration. *B*, records from the same fish beginning fifty-three minutes after transection, showing dyspneic periodicity giving way to weak, slow respiration.

more regular rhythm. The heart rate showed some irregular slowing but otherwise was generally more rapid, probably indicating a partial loss of vagus tone. In this fish the medullary centers remained reflexly functional for sixty minutes without a blood supply.

Discussion

The results reported above confirm Schoenlein (1895) insofar as an increase in the rate of flow of water to the gills caused an increase in respiratory rate. Springer (1928), working on *Mustelus canis* and *Squalus acanthias*, also reported that "the stronger the current the greater the rate of respiration." The marked, though rough, synchronism between the respiratory rate and the rate of the heart on altering the flow of water is difficult to understand, especially since the heart rate was changed about twice as much as the respiratory rate. It suggests a close nervous association between the respective medullary centers, although Lutz (1929) has found that each center may act independently. Inasmuch as accelerator nerves to the heart have not been demonstrated, the increase in heart rate accompanying increased respiration is probably due to inhibition of vagal tone. The vagus is known, under experimental conditions at least, to exert a continued influence on the heart (Lutz, 1930). Since *Scyllium* takes in water through the mouth on inspiration (Baglioni, 1907–08), a mechanism for increased respiration and heart rate during rapid swimming is clear.

That peripheral stimulation by water, however, is not necessary for continued regular respiration is obvious from Fig. 3. The inhibition on stopping the flow lasted only twelve seconds in this case, and ten seconds in the case illustrated in Fig. 4. This inhibition appears to be a transient reflex due to stimulation by collapse of the pharynx on stopping the flow of water. It occurred immediately, rather than after the water had been pressed out by several gill movements and air had entered, as suggested by Schoenlein (1895). Moreover, after the water had been expressed, a regular rhythm, rather than inhibition, was set up. It is apparent that, just as in the higher vertebrates, the rate of respiration is easily subject to peripheral control, but that a slow regular rhythm will continue without the usual peripheral stimulus.

The continuance of regular respiratory movements after transection of the aorta indicates an automaticity of the respiratory center without a blood supply. A rhythmic discharge from the cord in higher vertebrates has been found to occur under asphyxial conditions by Langendorff (1887) and by Brown-Séquard (1893), but the resulting movements are not considered to be true coördinated respiratory processes. In several teleosts Kolff (1908) noted the continuance of breathing movements for fifteen minutes after the heart had been removed. In the case of *Scyllium* with a transected aorta the regular rhythm which occurs at first, the onset of periodicity, and the subsequent dyspnea parallel the results of Baglioni (1907–08) with intact fishes in evacuated sea water. The usual explanation of periodicity involves alternate changes in the gas content of the blood flowing through the respiratory center. However, it appears that a periodic rhythmic discharge may occur without a blood supply, and therefore the cause for the periodicity must lie primarily within the nerve cells of the center.

Since it is impossible in the fish to cut the afferent fibers from the gills without destroying the motor pathways for respiration, conclusive proof of the automaticity of the respiratory center will be difficult to obtain. However, since rhythmic respiration continued after the water was stopped and the blood supply to the medulla interrupted, one may infer that, in fishes as in mammals, the respiratory center is autonomous. Furthermore, as in mammals, it is influenced by the gas content of the blood and by the peripheral stimulation.

Summary

1. The respiratory and cardiac responses to stopping and starting the water supply to the gills, to increasing and decreasing the rate of flow, and to complete interruption of the blood supply to the medulla of *Scyllium canicula* were recorded.

2. Sudden stopping and starting or increasing and decreasing the water supply evoked brief respiratory inhibition and sometimes ejection reflexes.

3. An increase in the rate of flow of sea water to the gills caused an increase in respiration and heart rates. A decrease caused the reverse. Too great an increase, however, evoked irregular inhibition.

4. Stopping the flow of water to the gills evoked brief inhibition of respiration followed by a regular rhythm at first, which sometimes became periodic and finally was interrupted by generalized muscular activity. The medullary centers remained reflexly functional for over three and one-half hours.

5. Interruption of the blood supply to the medulla when there was no water supply to the gills was followed by regular respiration at first, then periodicity and dyspnea. The medullary centers remained reflexly functional for over sixty minutes without a blood supply.

6. It is concluded that the respiratory center is autonomous, but that it is influenced by the gas content of the blood and by peripheral stimulation.

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